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Applying remote sensing to biodiversity science

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Abstract: Biodiversity is organized hierarchically from individuals to populations to major lineages in the tree of life. This hierarchical structure has consequences for remote sensing of plant phenotypes and leads to the expectation that more distantly related plants will be more spectrally distinct. Applying remote sensing to understand ecological processes from biodiversity patterns builds on prior efforts that integrate functional and phylogenetic information of organisms with their environmental distributions to discern assembly processes and the rules that govern species distributions. Spectral diversity metrics critical to detecting biodiversity patterns expand on the many metrics for quantifying multiple dimensions of biodiversity—taxonomic, phylogenetic, and functional—and can be applied at local (alpha diversity) to regional (gamma diversity) scales to examine variation among communities (beta diversity). Remote-sensing technologies stand to illuminate the nature of biodiversity-ecosystem function relationships and ecosystem service trade-offs over large spatial extents and to estimate their uncertainties. Such advances will improve our capacity to manage natural resources in the Anthropocene.

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Chapter 2

Applying Remote Sensing to Biodiversity Science



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and Jose Eduardo Meireles**

A treatment of the topic of biodiversity requires consideration of what biodiversity is, how it arises, what drives its current patterns at multiple scales, how it can be measured, and its consequences for ecosystems. Biodiversity science, by virtue of its nature and its importance for humanity, intersects evolution, ecology, conservation biology, economics, and sustainability science. These realms then provide a basis for discussion of how remote detection of biodiversity can advance our understanding of the many ways in which biodiversity is studied and impacts humanity. We start with a discussion of how biodiversity has been defined and the ways it has been quantified. We briefly discuss the nature and patterns of biodiversity and some of the metrics for describing biodiversity, including remotely sensed spectral diversity. We discuss how the historical environmental context at the time lineages evolved has left “evolutionary legacy effects” that link Earth history to the current functions of plants. We end by considering how remote sensing (RS) can inform our understanding of the relationships among ecosystem services and the trade-offs that are often found between biodiversity and provisioning ecosystem services.

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2.1 What Is Biodiversity?

Biodiversity encompasses the totality of variation in life on Earth, including its ecosystems, the species generated through evolutionary history across the tree of life, the genetic variation within them, and the vast variety of functions that each organism, species, and ecosystem possess to access and create resources for life to persist. Changes in the Earth's condition, including the actions of humanity, have consequences for the expression of biodiversity and how it is changing through time.

2.2 The Hierarchical Nature of Biodiversity

Since Darwin (1859), we have understood that biodiversity is generated by a process of descent with modification from common ancestors. As a result, biological diversity is organized in a nested hierarchy that recounts the branching history of species (Fig. 2.1a). Individual organisms are nested within populations, which are nested within species and within increasingly deeper clades. This hierarchy ultimately represents the degree to which species are related to each other and often conveys when in time lineages split (Fig. 2.1a).

Evolution results in the accumulation of changes in traits that causes lineages to differ. The degree of trait divergence between taxa is expected to be proportional to the amount of time they have diverged from a common ancestor. As a consequence, distantly related taxa are expected to be phenotypically more dissimilar (Fig. 2.1b).

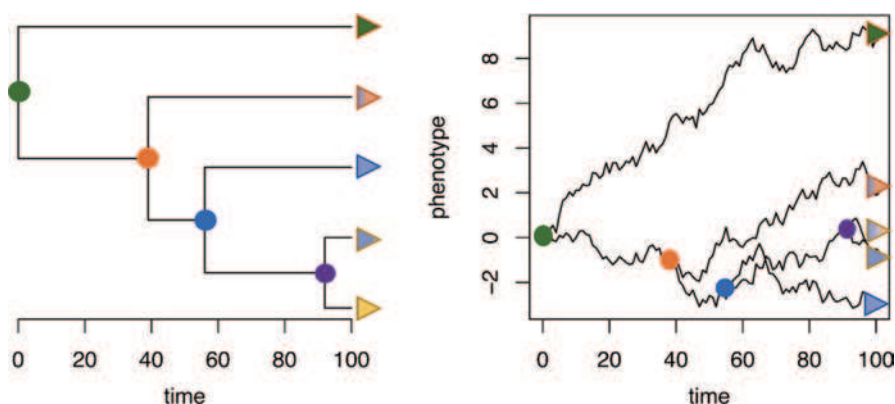


Fig. 2.1 (a) The hierarchical organization of biodiversity. Species (triangles) are nested within phylogenetic lineages (clades) due to shared ancestry. All species within a lineage have common ancestor (filled circles). (b) Differences in the phenotypes (or trait values) of species (triangles) tend to increase with time since divergence from a common ancestor, shown by the orange circle. The divergence points at which species split are shown in the simulation, and the filled circles indicate the common ancestor of each lineage

Since spectral signals are integrated measures of phenotype, spectra should be more dissimilar among distantly related groups than among close relatives (Cavender-Bares et al. 2016b; McManus et al. 2016; Schweiger et al. 2018). This expectation can be seen from models of evolution in which traits change over time following a random walk (Brownian motion process; Fig. 2.1b) (O'Meara et al. 2006; Meireles et al., Chap. 7). In cases of convergent evolution—where natural selection causes distant relatives to evolve similar functions in similar environments—however, phenotypes can be more similar than expected under Brownian motion.

This hierarchy of life is relevant to RS of plant diversity because certain depths of the tree of life may be more accurately detected than others at different spatial resolutions and geographic regions. For example, it could be easier to detect deeper levels in the hierarchy (such as genera or families) in hyper-diverse communities than in shallow levels (such as species) because deep splits tend to have greater trait divergence. Meireles et al. (Chap. 7) further explain why and how phylogenetic information can be leveraged to detect plant diversity.

2.3 The Making of a Phenotype: Phylogeny, Genes, and the Environment

The phenotype of an organism is the totality of its attributes, and it is quantified in terms of its myriad functions and traits. The phenotype of an organism is a product of the interaction between the information encoded in its genes—the genotype—and the environment over the course of development. Understanding the relative influence of gene combinations, environmental conditions, and ontogenetic stage is an active area of investigation across different disciplines (Diggle 1994; Sultan 2000; Des Marais et al. 2013; Palacio-López et al. 2015).

Although genotypes often play a critical role in determining phenotypic outcomes, many processes can result in mismatches between genotype and phenotype. One of the most well documented of these processes is known as phenotypic plasticity—when organisms with the same genotype display different phenotypes, usually in response to different environmental conditions (Bradshaw 1965; Scheiner 1993; Des Marais et al. 2013). Plasticity can also result in distinct genotypes developing similar phenotypes when growing under the same environmental conditions.

A similar story can be told about the relationship of phenotypic similarity and phylogenetic relatedness. As we have seen earlier, closely related taxa are expected to be more similar to each other than distantly related taxa. However, convergent evolution can lead to plants from different branches of the tree of life to evolve very similar traits—such as succulents, which are found within both euphorbia and very distantly related cacti taxa.

The fact that phenotypes can be, but not necessarily are, directly related to specific genotypes and phylogenetic history should be considered when remotely sensing biodiversity. Only phenotypes can be remotely sensed directly. Genetic and phylogenetic information can only be inferred from spectra to the degree that

absorption features of plant chemical or structural characteristics at specific wavelengths relate to phenotypic information. However, the effects plant traits have on spectra are only partially understood. Identifying the regions of the spectrum that are influenced by specific traits is complicated by overlapping absorption features and subtle differences in plant chemical, structural, morphological, and anatomical characteristics that simultaneously influence the shape of the spectral response (Ustin and Jacquemoud, Chap. 14).

2.4 Patterns in Plant Diversity

One of the most intensively studied patterns in biodiversity is the latitudinal gradient, in which low-latitude tropical regions harbor more species, genera, and families of organisms than high-latitude regions. In particular, wet tropical areas tend to reveal higher diversity of organisms than colder and drier climates (Fig. 2.2). Humboldt (1817) documented these patterns quite clearly for plant diversity. Naturalists since then have sought to explain these patterns.

Tropical biomes have existed longer than more recent biomes, such as deserts, Mediterranean climates, and tundra, which expanded as the climate began to cool some 35 million years ago. Tropical biomes also cover more land surface area than other biomes. Tropical species thus have had more time and area (integrated over the time since their first appearance) for species to evolve and maintain viable populations (Fine and Ree 2006). Lineages that originally evolved in the tropics may also have been less able to disperse out of the tropics and to evolve new attributes adapted to cold or dry climates—due to phylogenetic conservatism—restricting their ability to diversify (Wiens and Donoghue 2004). However, not all lineages follow this latitudinal gradient. Ectomycorrhizal fungi, for example, show higher diversity at temperate latitudes, where they likely have higher tree host density (Tedersoo and Nara 2010). Moreover, other measures of diversity do not necessarily follow these patterns. Variation in functional attributes of species, for example, follow different patterns depending on the trait (Cavender-Bares et al. 2018; Echeverría-Londoño et al. 2018; Pinto-Ledezma et al. 2018b). Specific leaf area, one of the functional traits that is highly aligned with the leaf economic spectrum (discussed below), shows higher variation at high latitudes than low latitudes across the Americas. In contrast, seed size shows higher variation at low latitudes (Fig. 2.2b).

At regional scales, variation in the environment, as discussed by Record et al. (Chap. 10), sets the stage for variation in biodiversity because species have evolved to inhabit and can adapt to different environments, which allows them to partition resources and occupy different niches created by environmental variation. Thus, habitat diversity begets biodiversity, and remotely sensed measures of environmental variation have long been known to predict biodiversity patterns (Kerr et al. 2001).

Land area is another long-observed predictor of species diversity, first described for species within certain guilds on island archipelagoes (Diamond and Mayr 1976).

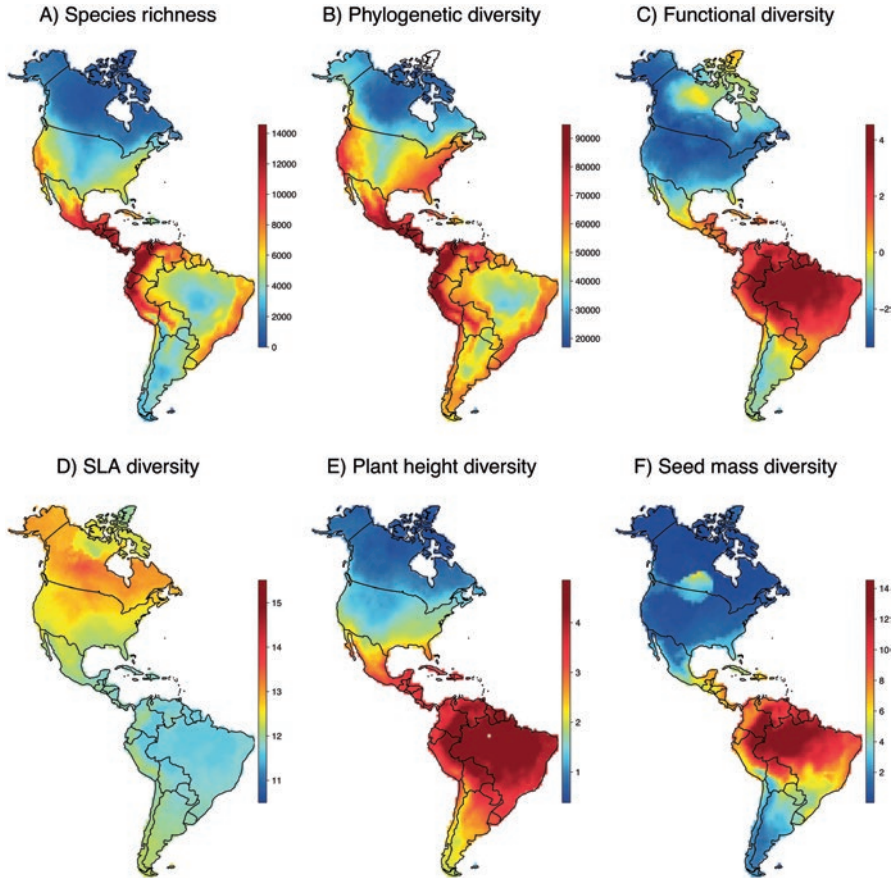


Fig. 2.2 Map of the Americas showing plant species richness, phylogenetic diversity, and functional diversity. Species richness and phylogenetic and functional diversities were estimated based on available information from the Botanical Information and Ecology Network (BIEN) database (Enquist et al. 2016, <https://peerj.com/preprints/2615/>). Distribution of functional diversity (trait mean) for three functional traits (**d–f**) was log-transformed for plotting purposes. (**a**) Species richness; (**b**) phylogenetic diversity; (**c**) first principal component of functional trait means; (**d**) specific leaf area (mm^2/mg); (**e**) plant height (m); and (**f**) seed mass (mg). Diversity metrics were calculated from an estimated presence-absence matrix (PAM) for all vascular plant species at 1 degree spatial resolution (PAM dimension = 5353 pixels \times 98,291 species) using range maps and predicted distributions. Functional diversity is based on the first principal component of a principal component analysis (PCA) of species means for the three functional traits

These observations led to the generalization that richness (number of species, S) increases with available land area (A), giving rise to the well-known species-area relationships, in which the log of species number increases linearly with the log of the area available:

$$\log(S) = z \times \log(A) + c, \quad (2.1)$$

or simply,

$$S = cA^z, \quad (2.2)$$

where c is the y-intercept of the log-log relationship and z is the slope.

2.5 Functional Traits, Community Assembly, and Evolutionary Legacy Effects on Ecosystems

2.5.1 *Functional Traits and the Leaf Economic Spectrum*

There is a long history of using functional traits to understand ecological processes, including the nature of species interactions, the assembly of species into ecological communities, and the resulting functions of ecosystems. Species with different functions are likely to have different performance in different environments and to use resources differently, allowing them to partition ecological niches. They are thus less likely to compete for the same resources, promoting their long-term coexistence. An increased focus on trait-based methodological approaches to understanding the relationship between species functional traits and the habitats or ecological niches was spurred by the formalization of the leaf economic spectrum (LES) (Wright et al. 2004). The LES shows that relationships exist among several key traits across a broad range of species and different climates (Reich et al. 1997; Wright et al. 2004) and that simple predictors, such as specific leaf area (SLA, or its reciprocal leaf mass per area, LMA) and leaf nitrogen content, represent a major axis of life history variation. This axis ranges from slow-growing (“conservative”) species that tolerate low-resource environments to fast-growing (“acquisitive”) species that perform well in high-resource environments (Reich 2014). Variations in relatively easy-to-measure plant traits are tightly coupled to hard-to-measure functions, such as leaf lifespan and growth rate, which reveal more about how a plant invests and allocates resources over time to survive in different kinds of environments. High correlations of functional traits provide strong evidence for trait coordination across the tree of life. The variation in plant function across all of its diversity is relatively constrained and can be explained by a few major axes of trait information (Díaz et al. 2015). Conveniently, traits such as SLA and N are readily detectable via spectroscopy. Other traits—such as leaf lifespan or photosynthetic rates—that are harder to measure but are correlated with these readily detectable traits can thus be inferred, permitting greater insight into ecological processes.

2.5.2 Plant Traits, Community Assembly, and Ecosystem Function

Considerable evidence supports the perspective that plant traits influence how species sort along environmental gradients and are linked to abiotic environmental filters that prevent species without the appropriate traits from persisting in a given location. Traits thus influence the assembly of species in communities—and consequently, the composition, structure, and function of ecosystems. Variation in traits among individual plants and species within communities indicates differences in resource use strategies of plants, which have consequences for ecosystem functions, such as productivity and resistance to disturbance, disease, and extreme environmental conditions. Moreover, the distribution of plant traits within communities influences resource availability for other trophic levels, above- and belowground, which affects community structure and population dynamics in other trophic levels. A major goal of functional ecology is to develop predictive rules for the assembly of communities based on an understanding of which traits or trait combinations (e.g., the leaf-height-seed (LHS) plant ecology strategy, sensu Westoby 1998) are important in a given environment, how traits are distributed within and among species, and how those traits relate to mechanisms driving community dynamics and ecosystem function (Shipley et al. 2017). This predictive framework requires selecting relevant traits; describing trait variation and incorporating this variation into models; and scaling trait data to community- and ecosystem-level processes (Funk et al. 2017). Selecting functional traits for ecological studies is not trivial. Depending on the question, individual traits or trait combinations can be selected that contribute to a mechanistic understanding of the critical processes examined. One can distinguish *response traits*, which influence a species response to its environment, and *effect traits*, which influence ecosystem function (Lavorel and Garnier 2002). These may or may not be different traits. Disturbance or global change factors that influence whether a species can persist within a habitat or community based on its response traits may impact ecosystem functions in complex ways (Díaz et al. 2013). Plant traits are at the heart of understanding how the evolutionary past influences ongoing community assembly processes and ecosystem function (Fig. 2.3). Traits also influence species interactions, which contribute to continuing evolution. Remotely sensed plant traits, if detected and mapped (Serbin and Townsend, Chap. 3; Morsdorf et al., Chap. 4) at the appropriate pixel size and spatial extent (Gamon et al., Chap. 16), can provide a great deal of insight into these different processes (Fig. 2.4).

2.5.3 Phylogenetic, Functional, and Spectral Dispersion in Communities

The rise of phylogenetics in community ecology was based on the idea that functional similarity due to shared ancestry should be predictive of environmental sorting and limiting similarity. These processes depend on physiological tolerances

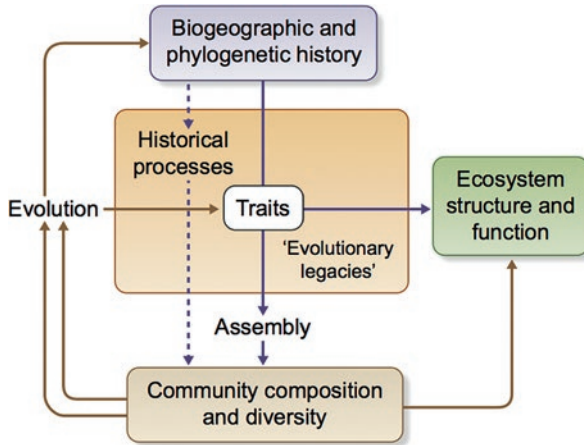


Fig. 2.3 Plant traits that have evolved over time influence how plants assemble into communities, which shapes ecosystem structure and function. Traits reflect biogeographic and environmental legacies and evolve in response to changing environments. They play a central role in ecological processes influencing the distribution of organisms and community assembly. A range of traits influence the way plants reflect light, such that many traits can be mapped continuously across large spatial extents with imaging spectroscopy. The remote detection of plant traits provides incredible potential to observe and understand patterns that reveal information about community assembly, changes in ecosystem function, and how legacies from the past shape community structure and ecosystem processes today. (Reprinted from Cavender-Bares et al. 2019, with permission)

in relation to environmental gradients and intensity of competition as a consequence of shared resource requirements (Webb 2000a, 2002). The underlying conceptual framework was formalized in terms of functional traits in individual case studies (Cavender-Bares et al. 2004; Verdu and Pausas 2007). The tendency to oversimplify the interpretation of phylogenetic patterns in communities, whereby phylogenetic overdispersion was equated with the outcome of competitive exclusion and phylogenetic clustering was interpreted as evidence for environmental sorting, led to a series of studies investigating the importance of scale (Cavender-Bares et al. 2006; Swenson et al. 2006) and the role of Janzen-Connell-type mechanisms, i.e., density-dependent mortality due to pathogens and predators (Gilbert and Webb 2007; Parker et al. 2015). Further developments revealed that the relationship between patterns and ecological processes is context-dependent—in particular, with respect to spatial scale (Emerson and Gillespie 2008; Cavender-Bares et al. 2009; Gerhold et al. 2015). Later studies revisited assumptions about the nature of competition and expected evolutionary and ecological outcomes (Mayfield and Levine 2010). Likewise, interpreting spectral dispersion will depend on the spatial resolution and pixel (grain) size of remotely sensed imagery relative to plant size (Marconi et al. 2019) as well as on the consideration of specific spectral regions and their functional importance. When traits and spectral regions are highly phylogenetically conserved (see Meireles et al., Chap. 7), trait, phylogenetic, and spectral data provide equivalent information. However, when some traits and spectral regions are

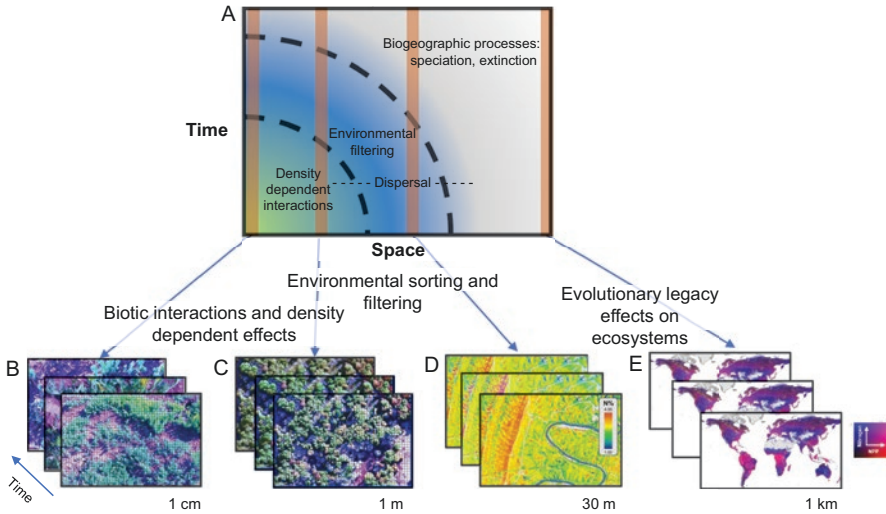


Fig. 2.4 (a) Biological processes change with spatial and temporal scale as do the patterns they give rise to. (Adapted from Cavender-Bares et al. 2009.) Detection and interpretation of those patterns will shift with spatial resolution (pixel size) and extent (b–e). (a) At high spatial resolutions (1 cm pixel size)—that allow detection of individual herbaceous plants and their interactions—and relatively restricted spatial extents in which the abiotic environment is fairly homogeneous, spectral dissimilarity among pixels may indicate complementarity of contrasting functional types. (b) The grain size sufficient to detect species interactions is likely to shift with plant size. For example, the interactions of trees in the Minnesota oak savanna and their vulnerability to density-dependent diseases, such as oak wilt (*Bretziella fagacearum*), can be studied at a 1 m pixel size. (c) At somewhat larger spatial resolution (30 m pixel sizes) and extent, environmental sorting—which includes interactions of species with both the biotic and abiotic environments—may be detected by comparing spectral similarity of neighbors and comparing mapped functional traits to environmental variation. Images adapted from Singh et al. (2015). The ability to detect change through time may be especially important in understanding species interactions and ecological sorting processes in relation to the biotic and abiotic environment. (d) At the global scale, it may be possible to detect the evolutionary legacy effects. For instance, regions with similar climate and geology can differ in vegetation composition and ecosystem function as a consequence of differences in which lineages evolved in a given biogeographic region and their historical migration patterns. Shown are mapped values of %N and NPP based on Moderate Resolution Imaging Spectroradiometer (MODIS) data. (Adapted from Cavender-Bares et al. 2016a)

conserved, but others related to species interactions or with the abiotic environment vary considerably among close relatives, there is the potential to tease apart spectral signals that may relate to species interactions.

Spatial patterns of spectral similarity and dissimilarity also have the potential to provide meaningful information about ecological processes and the forces that dominate community assembly at a particular scale. For example, to the extent that spectral similarity of neighboring plants can be determined, high spectral similarity might indicate that functionally and/or phylogenetically similar individuals are sorting into the same environment, while spectral dissimilarity might indicate that quite distinct individuals are able to coexist if they exhibit complementarity by

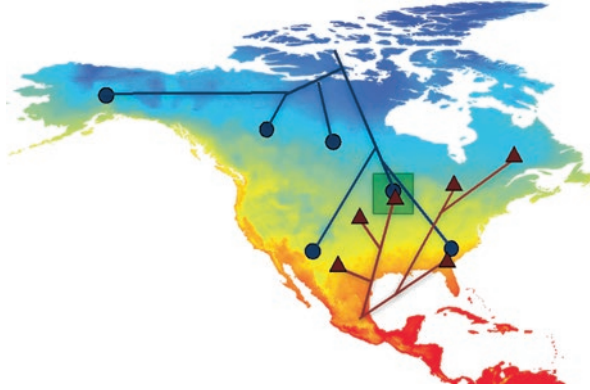


Fig. 2.5 Evolutionary legacy effects as a consequence of biogeographic origin. Two lineages are shown that have contrasting origins, one from the tropics and one from high latitudes. Both diversified and expanded to colonize intermediate latitudes such that their descendants sometimes co-occur. Lineages with ancestors from contrasting climatic environments likely differ in functional traits that reflect their origins and thus may assemble in contrasting microenvironments within the local communities where they co-occur. (Adapted from Cavender-Bares et al. 2016a)

partitioning resources. Approaches that use spectral detection of patterns that might be interpreted within this framework will need to pay close attention to the pixel-to-plant size ratio—or the grain size at which biological diversity varies (Gamon et al., Chap. 16; Serbin and Townsend, Chap. 3; Schimel et al., Chap. 19)—as well as to the spatial extent at which density-dependent processes and environmental sorting pressures are strongest. Often these processes are expected to dominate at different spatial scales, such that competition and Janzen-Connell-type mechanisms operate at very local scales, while environmental sorting may be more important at landscape scales. Other factors, such as the geographic locations and environmental conditions under which lineages diversified, may impact spectral patterns of phylogenetic, functional trait, and spectral similarity at continental scales (Fig. 2.5). At the same time, spectral similarity will be driven by similar ecological forces, since both genetic and phylogenetic compositions, as well as environmental factors, drive phenotypic variation that can be spectrally detected.

2.6 Evolutionary Legacy Effects on Ecosystems

Ecological communities are formed by resident species (incumbents) and colonizer species. Incumbents may have originated in the study region (or at least have had considerable time to adapt to their biotic and abiotic environment), whereas colonizers evolved elsewhere and subsequently dispersed into the region. However, the processes that determine species distributions and the assembly of ecological communities are complex. Species within communities experience unique combinations

of evolutionary constraints and innovations due to legacies of their biogeographic origins and the environmental conditions in which they evolved (Cavender-Bares et al. 2016a; Pinto-Ledezma et al. 2018a). Historical contingencies play a role in which lineages can take advantage of opportunities to diversify following climate change or other disturbances and environmental transitions. The rate of species range expansion and contraction and the evolution of species functional traits that allow species to establish and persist in some regions or under particular environmental conditions but not elsewhere are shaped by biogeographic history (Moore et al. 2018). For example, when species from two distinct lineages—one that evolved in tropical climates and the other that evolved in temperate climates—colonize a new environment, they are predicted to persist in contrasting microhabitats as a consequence of niche conservatism (Ackerly 2003; Harrison 2010; Cavender-Bares et al. 2016a). These evolutionary legacies—collectively referred to as “historical factors” (Ricklefs and Schluter 1993)—operate at different spatial and temporal scales that leave their imprints on species current functional attributes and distributions and consequently on ecosystem function itself (Fig. 2.4c, Cavender-Bares et al. 2016a). RS approaches can help reveal how the deep past has influenced current biodiversity patterns and ecosystem function by decoupling climate and geological setting from ecosystem function. Current and forthcoming RS instruments (Lausch et al., Chap. 13; Schimel et al., Chap. 19) enable the monitoring of plant productivity, dynamics of vegetation growth, seasonal changes in chemical composition, and other ecosystem properties independently of climate and geology. These technologies thus provide opportunities to detect how biodiversity is sorted across the globe and to determine how variable ecosystem functions can be in the same geological and environmental setting. Both are important for developing robust predictive models of how lineages respond to current and future environmental conditions with important consequences for managing ecosystems in the Anthropocene.

2.7 Quantifying Multiple Dimensions of Biodiversity

Several major dimensions of biodiversity have emerged in the literature that capture different aspects of the variation of life. *Taxonomic diversity* focuses on differences between species or between higher-order clades, such as genera or families. Estimating the numbers and/or abundances of different taxa across units of area captures this variation. *Phylogenetic diversity* captures the evolutionary distances between species or individuals, represented in terms of millions of years since divergence from a common ancestor or molecular distances based on accumulated mutations since divergence. *Functional diversity* focuses on the variation among species as a consequence of measured differences in their functional traits, frequently calculated as a multivariate metric but also calculated for individual trait variation. *Spectral diversity* captures the variability in spectral reflectance from vegetation (or from other surfaces), either measured and calculated among individual

plants or, more commonly, calculated among pixels or among other meaningful spatial units.

Biodiversity metrics can have different components, including (1) taxonomic units; (2) abundance, frequency, or biomass of those units and their degree of evenness; and (3) the dispersion or distances between those units in trait, evolutionary, or spectral space. Myriad metrics quantify the major dimensions and components of diversity. Here we briefly describe several frequently used metrics; the equation for each metric and the source citation that provides the full details are given in Table 2.1.

Table 2.1 A brief summary of metrics that are commonly used to estimate the diversity of different facets/dimensions of plant diversity

Metric	Equation	Definition	Reference
Whittaker alpha	α	Number of species found in a sample or particular area, generally expressed as species richness	Whittaker (1960)
Whittaker beta	γ/α	Variation of species composition between two samples. Can be interpreted as the effective number of distinct compositional units in the region	Whittaker (1960)
Whittaker gamma	γ	Overall diversity (number of species) within a region	Whittaker (1960)
Shannon's H	$-\sum_{i=1}^s p_i \ln p_i$	Metric that characterizes species diversity in a sample. Assumes that all species are represented in the sample and that individuals within species were sampled randomly	Shannon (1948)
Simpson's D	$\frac{1}{\sum_{i=1}^s p_i^2}$	Metric that characterizes species diversity in a sample. Contrary to Shannon's H, Simpson's D captures the variance of the species abundance distribution	Simpson (1949)
Faith's PD (phylogenetic diversity)	$\sum_{ecz(T)} \lambda e$	Sum of the lengths of all phylogenetic branches (from the root to the tip) spanned by a set of species	Faith (1992)
PSV (phylogenetic species variability)	$\frac{ntrC - \sum C}{n(n-1)} = 1 - \bar{c}$	Measures the variability in an unmeasured neutral trait or the relative amount of unshared edge length	Helmus (2007)
PSR (phylogenetic species richness)	$nPSV$	The deviation from species richness, penalized by close relatives	Helmus (2007)

(continued)

Table 2.1 (continued)

Metric	Equation	Definition	Reference
PSE (phylogenetic species evenness)	$\frac{m \text{diag}(C)' M - M'CM}{m^2 - \bar{m}_i m}$	PSV metric modified to account for relative species abundance or simply abundance-weighted PSV	Helmus (2007)
${}^qPD(T)$ (phylogenetic branch diversity)	$\left[\sum_{i=1}^B L_i x \left(\frac{a_i}{\bar{T}} \right)^q \right]^{\frac{1}{1-q}}$	Hill number (the effective total branch length) of the average time of a tree's generalized entropy over evolutionary time intervals	Chao et al. (2010)
${}^qD(T)$ (phylogenetic Hill numbers)	$\left(\frac{{}^qPD(\bar{T})}{\bar{T}} \right)$	Effective number of species or lineages	Chao et al. (2010)
FRic (functional richness)	Quickhull algorithm	Quantity of functional space filled by the sample. The number of species within the sample must be higher than the number of functional traits	Barber et al. (1996), Villegger et al. (2008)
FEve (functional evenness)	$\frac{\sum_{i=1}^{S-1} \min \left(PEW_i, \frac{1}{S-1} \right) - \frac{1}{S-1}}{1 - \frac{1}{S-1}}$	Quantifies the abundance distribution in functional trait space	Villegger et al. (2008)
FDiv (functional divergence)	$\frac{\Delta d + \overline{dG}}{\Delta d + \overline{dG}}$	Metric that measures the spread of species abundance across trait space	Villegger et al. (2008)
${}^qD(TM)$ (functional trait dispersion)	$1 + (S - 1) \times {}^qE(T) \times M'$	Metric that quantify the effective number of functionally distinct species for a given level of species dispersion	Scheiner et al. (2017)
β_{sor} (Sørensen pairwise dissimilarity)	$\frac{b + c}{2a + b + c}$	Compares the shared species relative to the mean number of species in a sample. Bray-Curtis dissimilarity is a special case of Sørensen dissimilarity that accounts for species abundance	Sørensen (1948), Baselga (2010)
β_{sim} (Simpson pairwise dissimilarity)	$\frac{\min(b, c)}{a + \min(b, c)}$	Similar to Sørensen dissimilarity but independent of species richness	Simpson (1943), Lennon et al. (2001), Baselga (2010)
β_{jac} (Jaccard index)	$\frac{a}{a + b + c}$	Metric that compares the shared species to the total number of species in all samples	Jaccard (1900)

2.7.1 *The Spatial Scale of Diversity: Alpha, Beta, and Gamma Diversity*

Diversity metrics are designed to capture biological variation at different spatial extents. Alpha diversity (α) represents the diversity within local communities, which are usually spatial subunits within a region or landscape. Whittaker first defined beta diversity (β) as the variation in biodiversity among local communities and gamma diversity (γ) as the total biodiversity in a region or a region's species pool (Whittaker 1960).

$$\beta = \frac{\gamma}{\alpha}, \quad (2.3)$$

where β is beta diversity, γ gamma diversity, and α alpha diversity.

Other authors have defined beta diversity differently (see Tuomisto 2010), including using variance partitioning methods (Legendre and De Cáceres 2013).

2.7.2 *Taxonomic Diversity*

Species richness is the number of species for a given area. It does not include abundance of individuals within species. However, the relative abundances, frequency, and biomass of species within a community matter in terms of capture rarity and evenness. Abundance-weighted metric, such as Simpson's diversity index (D), incorporates both richness and evenness. A set of indices based on Hill numbers—a unified standardization method for quantifying and comparing species diversity across samples, originally presented by Mark Hill (1973)—were refined by Chao et al. (2005, 2010). These are generalizable to all of the dimensions of diversity and consider the number of species and their relative abundances within a local community. Hill numbers require the specification of the diversity order (q), which determines the sensitivity of the metric to species relative abundance. Different orders of q result in different diversity measures; for example, $q = 0$ is simply species richness, $q = 1$ gives the exponential of Shannon's entropy index, and $q = 2$ gives the inverse of Simpson's concentration index.

2.7.3 *Phylogenetic Diversity*

Phylogenetic diversity (PD) considers the extent of shared ancestry among species (Felsenstein 1985). For example, a plant community composed of two species that diverged from a common ancestor more recently is less phylogenetically diverse than a community of two species that diverged less recently. Faith's (1992) metric of PD

sums the branch lengths among species within a community (from the root of the phylogeny to the tip). One feature of this metric is that it scales with species richness because as new species are added into the community, new branch lengths are also added. Other metrics were subsequently developed that calculate the mean evolutionary distances among species independently of the number of species [e.g., mean phylogenetic distance (MPD, Webb 2000b; Webb et al. 2002) or phylogenetic species variability (PSV), Helmus 2007]. Helmus (2007) developed two more phylogenetic diversity metrics that scale either with richness or by incorporating species abundances. Phylogenetic species richness (PSR) increases with the number of species, but reduces the effect of species richness proportionally to their degree of shared ancestry. Phylogenetic species evenness (PSE) is similar to PSV but includes abundances by adding individuals as additional tips descending from a single species node, with branch lengths of 0. Chao et al. (2010) defined the phylogenetic Hill number, ${}^qD(T)$, as the effective number of equally abundant and equally distinct lineages and phylogenetic branch diversity, ${}^qPD(T)$, as the effective total lineage length from the root node (i.e., the total evolutionary history of an assemblage) (Chao et al. 2014).

Phylogenetic endemism is another aspect of biodiversity that can be estimated from phylogenetic information and range maps of species (Faith et al. 2004). Phylogenetic endemism can be simply defined as the quantity of PD restricted to a given geographic area. This metric thus focuses on geographic areas, rather than on species, to discern areas of high endemism based on evolutionary history for conservation purposes.

2.7.4 Functional Diversity

Widely used metrics of functional diversity consider the area or volume of trait space occupied by a community of species, the distances of each species to the center of gravity of those traits, and the trait distances between species (Mouillot et al. 2013). Functional attribute diversity (FAD) is a simple multivariate metric calculated as the sum of species pairwise distances of all measured continuous functional traits (Walker et al. 1999). Vileger et al. (2008) developed a series of functional diversity metrics that incorporate trait dispersion and distance among species as well as species abundances, including functional richness (FRic), functional divergence (FDiv), and functional evenness (FEve). Building on the framework of Vileger et al. (2008), Laliberté and Legendre (2010) developed functional dispersion (FDis), a functional diversity metric that is independent of species richness and can include species relative abundances (Table 2.1).

Scheiner's functional trait dispersion [${}^qD(TM)$, Scheiner et al. 2017] calculates the effective number of species (or units) that are as distinct as the most distinct species (or unit) in that community. ${}^qD(TM)$ decomposes diversity estimates into three components: the number of units (S), functional evenness [${}^qE(T)$, the extent to which units are equally dispersed], and mean dispersion [M' , the average distance or the distinctiveness of these units]. Functional diversity measured as ${}^qD(TM)$ is maxi-

mized when there are more units in a community that are more equitably distributed (or less clumped) and more dispersed (or positioned further apart) in space. Like Chao's approach, ${}^qD(TM)$ includes Hill numbers (q), which allow weighting of abundances: small and large q values emphasize rare and common species, respectively. Like many other biodiversity metrics, ${}^qD(TM)$ can be calculated from pairwise distances among species or individuals; thus, the metric can be applied to estimate different dimensions of biodiversity, including functional, phylogenetic (Scheiner 2012; Presley et al. 2014) and spectral components (Schweiger et al. 2018).

Briefly, functional trait dispersion [${}^qD(TM)$] is calculated as:

$${}^qD(TM) = 1 + (S - 1) \times {}^qE(T) \times M' \quad (2.4)$$

where:

S = species richness

$E(T)$ = trait evenness

M' = trait dispersion

q = Hill number

2.7.5 Spectral Diversity

Like taxonomic, functional, and phylogenetic diversity, spectral diversity can be calculated in many different ways. Spectral alpha diversity metrics include the coefficient of variation of spectral indices (Oindo and Skidmore 2002) or spectral bands among pixels (Hall et al. 2010; Gholizadeh et al. 2018, 2019; Wang et al. 2018, the convex hull volume (Dahlin 2016) and the convex hull area (Gholizadeh et al. 2018) of pixels in spectral feature space, the mean distance of pixels from the spectral centroid (Rocchini et al. 2010), the number of spectrally distinct clusters or "spectral species" in ordination space (Féret and Asner 2014), and spectral variance (Laliberté et al. 2019). Schweiger et al. (2018) applied ${}^qD(TM)$ to species mean spectra and to individual pixels extracted at random from high-resolution proximal RS data. The second approach is independent of species identity and uses the same number of pixels per community for analysis. In this manner, the problem of diversity scaling with the number of species in a community is eliminated, and greater differences in reflectance spectra among pixels result in increased spectral diversity. Conceptually, spectral diversity metrics are versatile and can be tailored to match taxonomic or phylogenetic units, e.g., by using mean spectra for focal taxa, or to resemble functional diversity by selecting spectral bands that align with known absorption features for specific chemical traits or spectral indices that capture plant characteristics of known ecological importance. If measured at the appropriate scale (see Gamon et al. Chap. 16), spectral diversity can integrate the variation captured by other metrics of diversity and similarly predicts ecosystem function (Fig. 2.6).

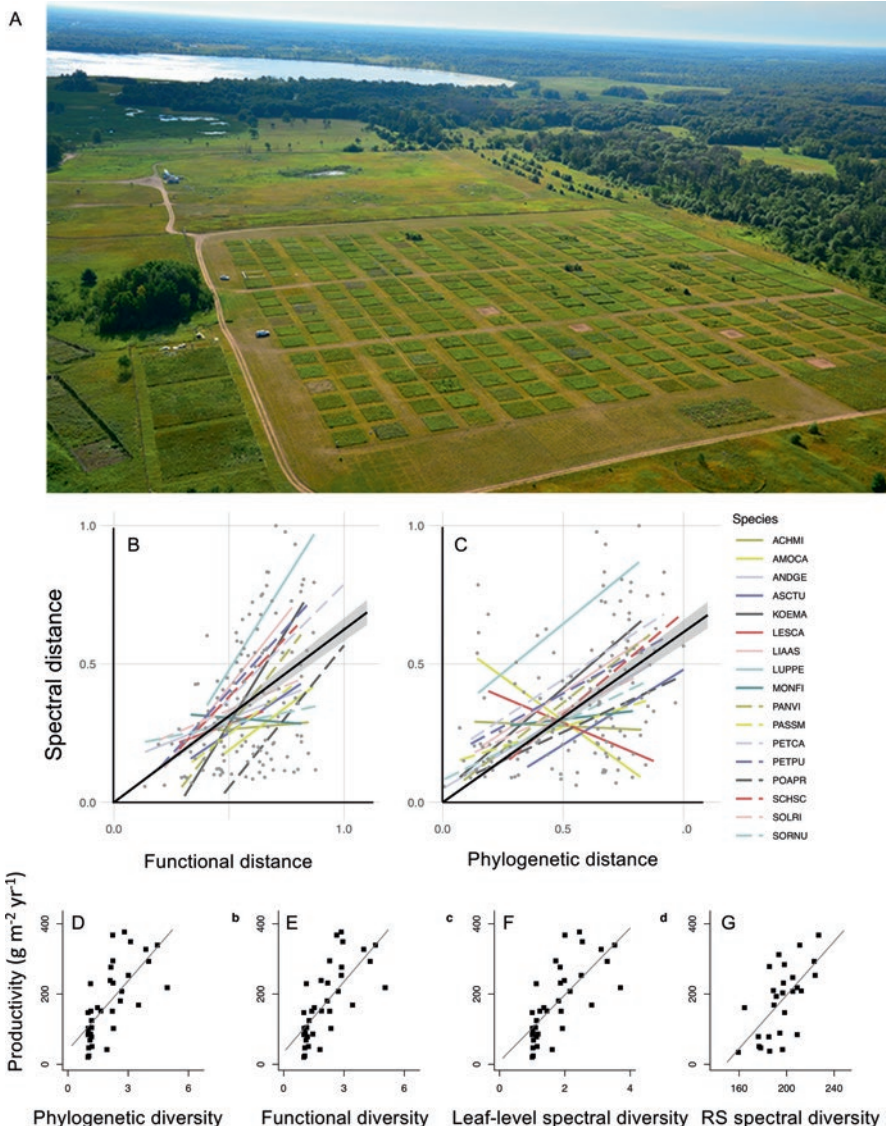


Fig. 2.6 (a) Aerial photo of the Cedar Creek long-term biodiversity experiment (BioDIV) (Courtesy of Cedar Creek Ecosystem Science Reserve). (b) Pairwise phylogenetic and (c) functional distances for the 17 most abundant prairie-grassland species in BioDIV are well-predicted by their spectral distances based on leaf-level spectral profiles (400–2500 nm). (d) Phylogenetic, (e) functional, and (f) leaf-level spectral diversities based on Scheiner's $^qD(TM)$ metric all predict ecosystem productivity in BioDIV. (g) Independent of information about species identities or their abundances, remotely sensed spectral diversity detected at high spatial resolution (1 mm) also predicts productivity. All graphs are redrawn from Schweiger et al. 2018. Species abbreviations in b and c are as follows: ACHMI = *Achillea millefolium* L., AMOCA = *Amorpha canescens* Pursh, ANDGE = *Andropogon gerardii* Vitman, ASCTU = *Asclepias tuberosa* L., KOEMA = *Koeleria macrantha* (Ledeb.) Schult., LESCA = *Lespedeza capitata* Michx., LIAAS = *Liatris aspera* Michx., LUPPE = *Lupinus perennis* L., MONFI = *Monarda fistulosa* L., PANVI = *Panicum virgatum* L., PASSMI = *Pascopyrum smithii* (Rydb.) Å. Löve, PETCA = *Petalostemum candidum* (Willd.), PETPU = *Petalostemum purpureum* (Vent.) Rydb., POAPR = *Poa pratensis* L., SCHSC = *Schizachyrium scoparium* Michx., SOLRI = *Solidago rigida* L., SORNU = *Sorghastrum nutans* (L.) Nash

2.7.6 *Beta Diversity Metrics*

Whittaker's 1960 definition of beta diversity (Eq. 2.3) quantified the degree of differentiation among communities in relation to environmental gradients. Under this definition, beta diversity is defined as the ratio between regional (gamma) and local (alpha) diversities (Eq. 2.3) and measures the number of different communities in a region and the degree of differentiation between them (Whittaker 1960; Jost 2007). Indices such as Bray-Curtis dissimilarity and Jaccard and Sørensen indices evaluate similarity of communities based on the presence or abundance of species within them. Metrics of similarity used for species have been adapted for phylogenetic and functional trait distances (Bryant et al. 2008; Graham and Fine 2008; Kembel et al. 2010; Cardoso et al. 2014) and can equally be applied to spectral information (Gamon et al., Chap. 16).

While the ratio between regional and local communities provides a simple means to estimate beta diversity, there are many different ways to calculate taxonomic, functional, and phylogenetic beta diversity that can be grouped into pairwise and multiple-site metrics (reviewed in Baselga 2010). Notably, beta diversity can be partitioned into components that capture species replacement—the “turnover component”—caused by the exchange of species among communities and differences in the number of species, the “nestedness component,” caused by differences in the number of species among communities. The turnover component can be interpreted as the difference between two community assemblages that contain contrasting subsets of species from a regional source pool, while the nestedness component represents the difference in species composition between two communities due to attrition of species in one assemblage relative to the other (Baselga 2010; Cardoso et al. 2014). Examining these different components of beta diversity for multiple dimensions of plant diversity provides a means to discern the role of historical and ongoing environmental sorting processes in the distribution of plant diversity at continental extents (Pinto-Ledezma et al. 2018b). In contrast to traditional diversity metrics, spectral diversity (alpha and beta) is only beginning to receive attention in biodiversity studies (Rocchini et al. 2018). Although different approaches have been proposed (Schmidtlein et al. 2007; Féret and Asner 2014; Rocchini et al. 2018; Laliberté et al. 2019), the estimation and mapping of dissimilarities in spectral composition (i.e., the variation among pixels) is similar to traditional estimations of beta diversity. For example, Laliberté et al. (2019) adapted the total community composition variance approach (Legendre and De Cáceres 2013) to estimate spectral diversity as spectral variance, partitioning the spectral diversity of a region (gamma diversity) into additive alpha and beta diversity components.

2.8 **Links Between Plant Diversity, Other Trophic Levels, and Ecosystem Functions**

Plant diversity has consequences for other trophic levels, sometimes reducing herbivory on focal species (Castagneyrol et al. 2014), but also increasing the diversity of insects and their predators in an ecosystem (Dinnage et al. 2012; Lind et al. 2015).

The distribution of plant traits within communities influences resource availability for other trophic levels above- and belowground, which affects community assembly and population dynamics across trophic levels. Diversity of neighbors surrounding focal trees can both increase and decrease pathogen and herbivore pressure on them (Grossman et al. 2019). Thus, while we know that plant diversity impacts other trophic levels, consistent rules across the globe that explain how and why these impacts occur remain elusive. An increasing number of studies reveal that plant diversity influences belowground microbial diversity and composition (Madritch et al. 2014; Cline et al. 2018). While these relationships are significant, they may explain limited variation given the number of other factors that influence microbial diversity and potentially due to a mismatch in sampling scales. Ultimately, it appears that chemical composition and productivity of aboveground components of ecosystems that can be remotely sensed are critical drivers of belowground processes, including microbial diversity (Madritch et al., Chap. 8).

Biodiversity loss is known to substantially decrease ecosystem functioning and ecosystem stability (Cardinale et al. 2011; O'Connor et al. 2017). Yet, the nature and scale of biodiversity-ecosystem function relationships remains a central question in biodiversity science. The issue is one that is ready to be tackled across scales using RS technology. The long-term biodiversity experiment at Cedar Creek Ecosystem Science Reserve (Tilman 1997) (Fig. 2.6), for example, has revealed the increasing effects of biodiversity on productivity over time (Reich et al. 2012) and that phylogenetic and functional diversity are highly predictive of productivity (Cadotte et al. 2008; Cadotte et al. 2009). Remotely sensed spectral diversity also predicts productivity (Sect. 2.9). Increased stability has also been linked to both higher plant richness (Tilman et al. 2006) and phylogenetic diversity (Cadotte et al. 2012) in this experiment. Tree diversity experiments show similar effects of increasing productivity with diversity (Tobner et al. 2016; Grossman et al. 2017) (Fig. 2.7), and these same trends emerge as the dominant pattern in forest plots globally

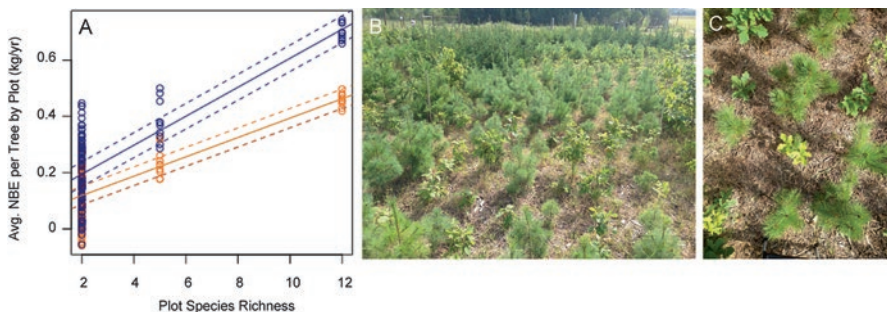


Fig. 2.7 The Forest and Biodiversity (FAB) experiment at the Cedar Creek Ecosystem Science Reserve shows overyielding (a)—greater productivity than expected in species-rich communities compared to monocultures—also called the net biodiversity effect (NBE). Curves show 90% predictions from multiple linear regression models (yellow 2013–2014; blue 2014–2015). (Redrawn from Grossman et al. 2018.) Photos (b, c) show juvenile trees grown in mixtures with varying neighborhood composition. The first phase of the experiment, shown here, includes three 600 m² blocks, each consisting of 49 plots (9.25 m²) planted in a grid with 0.5 m spacing

(Liang et al. 2016). Hundreds of rigorous biodiversity experiments have been designed and conducted to tease apart effects of changing numbers of species (richness) from effects of changing identities of species (composition) (O'Connor et al. 2017; Grossman et al. 2018; Isbell et al. 2018). Complementarity among diverse plant species that vary in their functional attributes and capture and respond to resources differently is the primary explanation for increasing productivity with diversity (Williams et al. 2017). Nevertheless, both the nature of biodiversity-ecosystem function (BEF) relationships and their causal mechanisms remain variable and scale dependent in natural systems. In the Nutrient Network global grassland experiments, in which communities have assembled naturally, the relationship between diversity and productivity is variable (Adler et al. 2011). In tropical forest plots around the globe, at spatial extents of 0.04 ha or less, the biodiversity-productivity relationship is strong. However, as scales increase to 0.25 or 1.0 ha, the relationship is no longer consistently positive and can frequently be negative (Chisholm et al. 2013). These varied relationships at contrasting spatial scales may result from nonlinear, hump-shaped relationships between biodiversity and ecosystem function across resource availability gradients as the nature of species interactions and their level of complementarity shift (Jaillard et al. 2014). RS methods—including imaging spectroscopy and LiDAR—that can detect both the diversity and the structure and function of ecosystems (Martin, Chap. 5; Atkins et al. 2018) can discern these relationships across spatial extents and biomes in natural systems. They thus have high potential to enhance our understanding of the scale and context dependence of linkages between biodiversity and ecosystem function (Grossman et al. 2018).

2.9 Incorporating Spectra into Relationships Between Biodiversity and Ecosystem Function

Detection of spectral diversity, in particular, offers the potential to contribute to the quantification of BEF relationships at large scales (Schweiger et al. 2018) and is thus worth discussing in more detail. The variability captured by spectral diversity in a given ecosystem depends on the way the spectral diversity is calculated, as well as its spatial and spectral resolution (Sect. 2.7.5; Gamon et al., Chap. 16). From a functional perspective, spectral profiles measured at the leaf level depend on the chemical, structural, morphological, and anatomical characteristics of leaves (Ustin and Jacquemoud, Chap. 14). Variation in spectra and spectral diversity can be used to test hypotheses about how specific traits influence ecosystem function, community composition, and other characteristics of ecosystems, when using spectral bands or spectral indices with known associations with specific plant traits (Serbin and Townsend, Chap. 3). Moreover, spectral bands and indices can be weighted based on prior information about the relative contribution of individual traits to specific ecosystem characteristics. However, while the absorption features

of some chemical traits are known, the effects of other, particularly nonchemical, plant traits on spectra are less well understood, in part due to overlapping spectral features and challenges associated with accurately describing nonchemical traits (Ustin and Jacquemoud, Chap. 14). Using the full spectral profile of plants in spectral diversity calculations provides a means to integrate chemical, structural, morphological, and anatomical variation and to acknowledge the many ways plants differ from one another.

It is certainly more complicated to decipher the biological meaning of spectral diversity calculated from spectral profiles than from measures of biodiversity that are based on a specific set of plant traits or spectral bands or indices with known links to specific traits. However, the variance that is explained by models based on spectral profiles can be partitioned into known and unknown sources of variation. This provides a means to assess the relative contribution of traits with known spectral characteristics and traits that are less well understood spectrally or that are of yet-unrecognized importance. At the canopy level, when spectra are measured from a distance, the question of what spectra and spectral diversity represent is further complicated by the influences that plant architecture, soil, and other materials have on the spectral characteristics of image pixels (Wang et al. 2018; Gholizadeh et al. 2018). Again, the degree to which these characteristics matter for a particular ecosystem needs to be evaluated in the particular context of the study. Some ecosystem components such as shade, soil, rock, or debris, which influence remotely sensed spectra, are biologically meaningful because they influence light availability and microclimate and provide resources for other trophic levels.

The association between plant spectra and traits can be illustrated by plotting spectral distances against functional distances or dissimilarity, as illustrated using species from the Cedar Creek biodiversity experiment (Fig. 2.6d). Given that functional differences among species are expected to increase with evolutionary divergence time (Fig. 2.1b), positive relationships are also expected among spectral and phylogenetic distances. The observed associations among spectral, functional, and phylogenetic dissimilarity (Fig. 2.6a, b) allow biodiversity metrics based on any of these dimensions of biodiversity to explain a similar proportion of the total variability in aboveground productivity (Fig. 2.6c–e), which is known to increase with the functional diversity of the plant community in this system (Cadotte et al. 2009). The species in the biodiversity experiment at Cedar Creek are relatively functionally dissimilar and distantly related, such that spectral, functional, and phylogenetic diversity also predict species richness (not shown). One advantage of spectral diversity is that the metric can be calculated from remotely sensed image pixels without depending on information about the distribution and abundance of species in an area, their functional traits, or phylogenetic relationships (Schweiger et al. 2018). By extracting a random number of high-resolution image pixels in each plant community, Schweiger et al. (2018) found that remotely sensed spectral diversity explained the biodiversity effect on aboveground productivity about as well as spectral diversity calculated using leaf-level spectra (Fig. 2.6).

2.10 Links Between Biodiversity and Ecosystem Services

Humans benefit from ecosystem functions and biodiversity. The benefits we derive from nature, often called ecosystem services, are a product of the biodiversity— assembled over millions of years—and ecosystem properties of a given region, or the whole Earth (Daily 1997). Daily (1997) defines ecosystem services as “the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life.” Ecosystem services, referred to by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as “nature’s contributions to people” (Díaz et al. 2018), are a socioecological concept that emerged from the Millennium Ecosystem Assessment (2005) and include provisioning, regulating, supporting, and cultural services. Some ecosystem service categories include direct benefits of biodiversity—through the use and spiritual values that humans establish with elements of biodiversity and ecosystems—and indirect benefits through the contributions of biodiversity to critical regulating ecosystem functions. The diversities of functional traits of plants make up the primary productivity of life on Earth and are essential to the ecosystem services on which all life depends. Assessment of ecosystem services depends on understanding both the ecosystem functions on which ecosystem services are derived and how services are valued by humans (Schrodt et al., Chap. 17). Modeling efforts that incorporate remotely sensed data can be used to describe ecosystem functions and quantify the services they generate (Sharp et al. 2018). (For modeling tools that enable mapping and valuing ecosystem services, see <https://naturalcapitalproject.stanford.edu/invest/>.)

2.11 Trade-Offs Between Biodiversity and Ecosystem Services

Biodiversity—as well as many regulating services to which biodiversity contributes and upon which it depends—frequently shows a negative trade-off with provisioning ecosystem services, such as agricultural production (Haines-Young and Potschin 2009). The nature of these trade-offs depends on the biophysical context, including the climate, soils, hydrology, and geology, and will differ among regions. A trade-off curve represents the limits set by these biophysical constraints and can be thought of in economic terms as an “efficiency frontier” that sets the boundaries on possible combinations of biodiversity (or regulating services) and provisioning services (Polasky et al. 2008). Combinations above the curve are not possible; outcomes beneath the curve provide fewer total benefits than what is actually possible from the environment. Quantifying the biodiversity and ecosystem service potential from land and how they trade off are critical to efficient management of ecosystems. Current RS tools and forthcoming technologies are well-poised to decrease uncertainty in estimates of biodiversity—ecosystem service trade-offs—and can

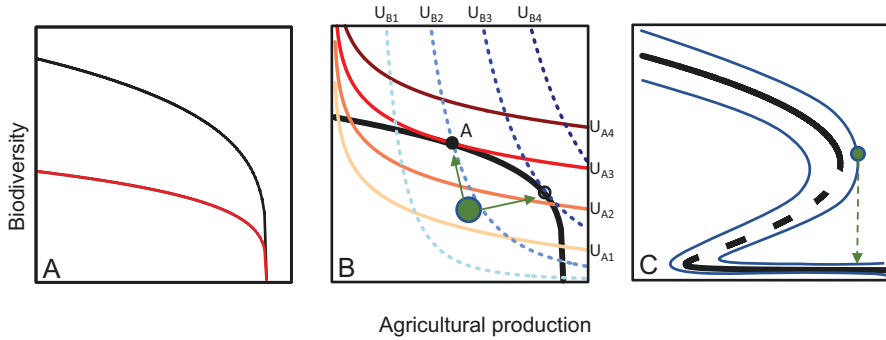


Fig. 2.8 RS technologies that enable detection of biodiversity and ecosystem functions aid in modeling their trade-offs. (a) The “efficiency frontier,” or biophysical constraints that limit biodiversity and crop production, depends on the specific climatic, historical, and resource context of the land area and on the growth or replenishment rate of the natural system. These constraints can vary among ecosystems (red vs black curves). (b) Where along the efficiency frontier we want to manage for depends on human values. The superimposed curves show isolines of equal utility (U_{A1-4} or U_{B1-4}) for two different stakeholders (A and B) who have sharply different willingness to give up natural habitat for crop production and vice versa. Utility—or benefits to each stakeholder—increases moving from yellow to dark red. The two points at which the highest utility curve for each stakeholder intersects with the efficiency frontier represent the greatest feasible benefit to the stakeholder (points A and B). Often ecosystems are managed well below the efficiency frontier (green circle). RS may enable detection of components of biodiversity and ecosystem services at relevant spatial scales that can inform stakeholders about improved outcomes and aid negotiation among stakeholders. (c) Some trade-offs can have thresholds and tipping points that, once traversed, may result in a degraded alternative state. RS approaches that can aid in predicting uncertainties and temporal variability in trade-offs, indicated by thin blue lines, can help maximize ecosystem service benefits without overshooting thresholds that risk pushing the system into a degraded state. (Adapted from Cavender-Bares et al. 2015b)

contribute meaningfully to decision-making and resource management (Chaplin-Kramer et al. 2015; de Araujo Barbosa et al. 2015; Schrodt et al., Chap. 17).

Where along the efficiency frontier we wish to target our management efforts depends on human preferences. These can differ strongly among different stakeholders that have contrasting priorities (Cavender-Bares et al. 2015a, b). Distinguishing the biophysical limits of ecosystems from contrasting stakeholder preferences for what they want from ecosystems is a critical contribution to participatory processes that enable dialogue and progress toward sustainability (Cavender-Bares et al. 2015b; King et al. 2015). RS technologies that can enhance detection of biodiversity as well as both regulating and provisioning ecosystem services—and changes in these at multiple scales—can thus increase clarity in decision-making processes in the face of rapid global change (Fig. 2.8).

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